Height is more important than light in determining leaf morphology in a tropical forest

Running title: *Height determines LMA*

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ABSTRACT

Both within and between species, leaf physiological parameters are strongly related leaf dry mass per area (LMA, g m^{-2}), which has been found to increase from forest floor to canopy top in every forest where it has been measured. Although vertical LMA gradients in forests have historically been attributed to a direct phenotypic response to light, an increasing number of recent studies have provided evidence that water limitation in the upper canopy can constrain foliar morphological adaptations to higher light levels. We measured height, light and LMA of all species encountered along 45 vertical canopy transects across a Costa Rican tropical rain forest. LMA was correlated with light levels in the lower canopy until approximately 18 m sample height and 22 % diffuse transmittance. Height showed a remarkably linear relationship with LMA throughout the entire vertical canopy profile for all species pooled and for each functional group individually (except epiphytes), possibly through the influence of gravity on leaf water potential and turgor pressure. Models of forest function may be greatly simplified by estimating LMA-correlated leaf physiological parameters solely from foliage height profiles, which in turn can be assessed with satellite- and aircraft-based remote sensing.

Key words: leaf mass per area, specific leaf area, sun leaves, shade leaves, water potential, vertical gradient, light environment, foliar morphology, turgor pressure, tropical rain forest

INTRODUCTION

Both within and across species, the physiology and function of leaves strongly relates to leaf mass per area (LMA, g m^{-2}), the product of leaf thickness and leaf density. Patterns of LMA can depend on both genotypic (across species) and phenotypic (within species) phenomenon. Across different species, LMA correlates with leaf life span, photosynthesis, dark respiration, and foliar N, describing the trade-off between long-lived leaves with greater allocation to structural rather than metabolic components vs. short-lived leaves with high metabolic activity and less physical protection (i.e. low LMA is associated with high photosynthetic capacity and vice-versa) (Reich et al. 1991).

Within species, however, the patterns between LMA and physiological function within the canopy profile can be quite the opposite. For example, LMA and photosynthesis per unit leaf area tend to be positively correlated and together increase from forest floor to canopy top (Bond et al. 1999). LMA increases within the vertical canopy profile in every forest where it has been measured; a kilogram of leaves at the bottom of a tree canopy generally has 3-5 times the surface area of the same mass of leaves at the top of the canopy (Hutchison et al. 1986, Oberbauer and Strain 1986, Hollinger 1989, Niinemets and Kull 1995, Meir et al. 2001). Why do we find this strong pattern of LMA within the canopy profile?

The study of leaf morphology and its response to environmental factors goes back more than a century, with investigations of light, evaporating power of air, temperature, humidity and wind as primary factors of influence on LMA (Hanson 1917). Classic studies have shown that, as a response to increased total irradiance, new leaves develop with longer, stacked palisade cells and larger and more mesophyll cells, thus increasing leaf thickness and LMA (Nobel 1977, Smith and Nobel 1978, Chabot et al. 1979, Oquist et al. 1982, Ellsworth and Reich 1992, Hikosaka et al. 1994). As a result of these early investigations, vertical gradients of LMA within forest stands have long been assumed to be primarily driven by the gradient of light from the ground to the canopy top (Jackson 1967, Hutchison et al. 1986, Oberbauer and Strain 1986, Hollinger 1989, Niinemets and Kull 1995, Meir et al. 2001). More recently, several studies have suggested that vertical gradients of hydrostatic constraints may be a primary determinant of patterns in LMA within the canopy profile (Niinemets 1997, Niinemets and Kull 1998, Marshall and Monserud 2003, Koch et al. 2004, Woodruff et al. 2004, England and Attiwill 2006, Ryan et al. 2006, Ishii et al. 2007, Ishii et al. 2008, Meinzer et al. 2008). Vertical species replacement may also contribute to patterns of LMA within forest canopy profiles, where an increase in height may correspond to the replacement of shade tolerant species (generally lower LMA) with shade intolerant species (generally higher LMA) (Niinemets and Kull 1998).

We investigated the sources of variation in LMA within the vertical canopy profile for all plant functional groups found in an old-growth tropical wet forest. If the pattern in LMA was primarily genotypic, as the result of species replacement within the canopy, we would expect plant functional groups lower in the canopy to have lower LMA overall than functional groups higher in the canopy. If the variation in LMA were primarily the result of phenotypic responses to light, we would expect to see a strong relationship between LMA and light environment. If the pattern in LMA were primarily a phenotypic response to gravity, we would expect to see a stronger relationship between LMA and sample height above the ground. This study presents results from a two year field campaign where we measured light environment, height and LMA of all plant functional groups (200+ species) found along 45 vertical canopy transects. We used a portable scaffolding tower to access foliage from forest floor to canopy top randomly across the landscape of an old-growth tropical rain forest in Costa Rica.

MATERIALS AND METHODS

Study site

We sampled in the old-growth forest of La Selva Biological Station, in the Caribbean lowlands of Costa Rica (elevation 37-150 m, 10°20’ N, 83°50’ W). La Selva is a tropical wet forest (Hartshorn 1983), with mean annual rainfall of 4000 mm, and a mean annual temperature of 26 ºC. The average canopy height for the old-growth forest (including gaps) is ~20 m, and individual emergent trees range from 30-60 m (Clark et al. 2004). For a more complete analysis of the forest canopy structure at La Selva, including leaf area distribution by height and functional group, see Clark et al. (2008). Woody plant diversity is approximately 90-115 spp ha^{-1}, based on studies reporting stems at least 10 cm in diameter (Hartshorn 1983, Lieberman et al. 1996). Both woody and herbaceous functional groups reach great heights in the canopy, and some epiphytes and ferns grow high in the canopy without being rooted in the ground. Additional information about the soils and plants of La Selva can be found in McDade et al. (1994).

Sampling design and data collection

The towers sampling design and construction were part of a larger project with the goal of characterizing tropical rain forest canopy structure and function across environmental gradients. Forty-five tower sites were located across the old-growth forest of La Selva using a stratified random sample (Clark et al. 2008). At each site, we constructed an aluminum walk-up scaffolding tower (Upright, Inc, Dublin, Ireland) to the top of the canopy, harvesting all foliage above each tower section as the tower was built. Tower heights varied from 1.86 m (1 section) to 44.64 m (24 sections). Our unique sample design offered completely random vertical transects of foliage within 4.56 m^2 area footprints, rather than the standard "whole tree" ecophysiology approach. Because of this design and the high biodiversity of the sampled ecosystem, we found very few species with enough samples in enough light or height environments to analyze individually, so we aggregated species into plant functional groups and also all species together for most of the analyses in this study (See Appendix, Fig. 2 for individual species plots for the only six species with >30 sample points at > 4 sample heights).

Foliage was separated into five plant functional groups: trees, palms, lianas, herbaceous groups (vines, forbs, and terrestrial ferns), and epiphytes (including epiphytic ferns). A subsample of leaves from each section and functional group was measured for leaf area (Li-3100, Li-Cor Inc., Lincoln, NE), and dried to constant mass at 60 °C to determine LMA (g m^{-2}). These data represent samples from over 200 species and over 58 families; 61 % were tree species, 12 % were palms, 10 % were lianas, 18 % were herbaceous groups, and 7 % were epiphytes.

The transmittance of diffuse light (% TRANS) above each sampled tower section (every 1.86 m) was measured with an LAI-2000 (LI-COR Inc., Lincoln, NE). LAI-2000 measurements were taken in two-sensor mode, with one sensor above the canopy and the other measuring below the canopy at dawn or when sky was completely overcast. We used a 180° view cap to block the tower itself from the view field. Percent diffuse transmittance was also measured at each tower with hemispherical photography (see Clark et al. for details, 2008). Both LAI-2000 and hemispherical photography methods yielded similar patterns with both height (Appendix, Fig. 1), and LMA (data not shown), therefore only one method of light measurement is presented here to avoid redundancy. A methodological comparison study showed % TRANS measured with an LAI-2000 to be closely related to the seasonally integrated photosynthetic photon flux density in a temperate deciduous forest (Gendron et al. 1998).

Statistical analyses

For all functional groups pooled and each group separately, we modeled LMA vs. sample height with simple linear regressions [LMA = $\beta_0 + \beta_1$ height], and LMA vs. light with log-linear regressions [LMA = $\beta_0 + \beta_1$ ln(light)]. Linear piece-wise regression procedures were also used to model LMA vs. light as in Ishii et al. (2008) to determine the light value at which foliage may not respond to increasing light levels. The light term was log-transformed because light showed a curved, asymptotic relationship with LMA, and the natural log function enabled us to linearize the model to combine both height and light terms into linear multiple regressions [LMA = $\beta_0 + \beta_1$ height + β_2 ln(light)] for each functional group individually. Interaction terms were not significant and were omitted from all models. In order to more clearly see patterns in the large dataset, we computed LMA means and standard errors for all functional groups combined and each group individually for the following height classes: 0-5, 5-10, 10-15, 15-20, 20-25, 25-30, and 30-40 m, and the following light classes: 0-5, 5-10, 10-15, 15-20, 20-30, 30-40, 40-50, 50-60, 60-70, 70-80, 80-90, and 90-100 % diffuse transmittance (%TRANS). We compared models for each functional group using partial R^2 values and standardized Akaike's Information Criterion ($AIC-AIC_{min}$, the AIC of the model minus the minimum AIC, zero for the best model) (Burnham and Anderson 1998).

Height and light are correlated within forest canopies (within our sample: ln(light) = 0.51 + height*0.11, $R^2 = 0.50$, $p<0.0001$, Appendix, Fig. 1). To address the possibility of collinearity in our models, we computed a variance inflation factor (VIF) between height and ln(light). The VIF quantifies the extent to which multicollinearity amongst the independent variables may be inflating their standard errors, making them less precise and difficult to interpret. A value of VIF close to 1 indicates the measurements represent different entities, and VIFs greater than 10 indicate serious collinearity (Chatterjee and Price 1991). To further separate out the effects of height and light, we grouped the pooled data into three narrow bands of height (0-2, 9-11, and 24-26 m) and plotted LMA vs. ln(light), and vice versa for three narrow bands of light transmittance (0-10, 30-40, and 90-100 % TRANS). Group categories were selected that had sufficient data ($n>40$) to represent low, medium, high levels of light and height. All statistical analyses were performed with SAS Version 9.1 (SAS Institute Inc., Cary, NC, USA).

RESULTS

Rooted herbaceous functional groups and palms were generally found in the lower canopy and the forest floor (mean sample heights = 7.3 ± 0.6 m and 8.5 ± 0.5 m, respectively); epiphytes and trees were found in the mid to upper canopy (14.4 ± 0.7 m and 15.3 ± 0.4 m, respectively); and lianas leaves were primarily found in the upper canopy (17.4 ± 0.7 m, Fig. 1A). LMA showed a different pattern with functional group, however. Rooted herbaceous groups had the lowest overall LMA (59.0 ± 2.4 g cm^{-2}), palms and epiphytes had the highest LMA (97.2 ± 2.6 g cm^{-2} and 90.1 ± 4.6 g cm^{-2}, respectively), and LMA means for trees and lianas fell somewhere in the middle (86.1 ± 1.7 g cm^{-2} and 85.3 ± 2.5 g cm^{-2}, respectively, Fig. 1B)

LMA increased linearly with height (R^2=0.27, p<0.0001, Fig. 2A), while the relationship between LMA and light was non-linear and weaker (R^2=0.16, p<0.0001, Fig. 2B, see Table 1 for regression equation coefficients under "All groups"). Linear piece-wise regression showed that LMA did not respond to light at values above 21.7 % TRANS (for light < 21.7: LMA = 2.3*light + 63.2; and for light ≥ 21.7: LMA= -0.007*light + 113.4), which corresponded to a canopy height of 17.7 m on average (Appendix, Fig. 1). When the LMA data from our stratified random sample of 45 vertical canopy transects were pooled across all five plant functional groups and separated into classes of height and light, the incredible uniformity of pattern with height was more apparent (Fig. 2C), and it was more apparent that LMA did not respond to light above approximately 20 % TRANS (Fig. 2D). Standard errors increased higher in the canopy because of decreased sample size for higher height and light classes (Figs. 2C-D).

LMA increased linearly with height for each functional group individually (Figs. 3A-J), while the relationship between LMA and light was non-linear for each group (Figs. 3K-T, see Table 1 for regression coefficients). Overall, LMA ranged from about 10 to 400 g m^{-2}, with outliers in the upper range almost exclusively comprised of epiphytes (Figs 3E and 3O). We found only six individual species with enough data points to statistically test in the same manner (>30 sample points at >4 sample heights), and results were very similar (Appendix, Fig. 2). Based on R^2 values, height explained more of the variance in LMA than light for all functional groups except epiphytes (Fig. 3, Table 1). Based on partial R^2 values, adding ln(light) to the "height only" models showed only marginal or no improvement in model R^2 values (Table 1). Adding height, on the other hand, showed 0.16 - 0.30 improvements in R^2 over the "light only" model in all groups except epiphytes (Table 1). Standardized AIC values for three competing models (height only, light only, height+light) showed that for all plant functional groups except epiphytes, light did not greatly improve the model fit once height was included in the model (Fig. 4, Table 1). The model with light only was the worst fit for all groups except epiphytes ($AIC-AIC_{min}$=zero for the best model fit, Fig. 4). For all groups pooled, residuals of the "Height only" model were plotted against ln(light) and residuals of the "Light only" model were plotted against sample height (Appendix, Fig. 3). After the variance in LMA was explained by height, there was little left to be explained by light ($p=0.2$), but height still added additional information after the variance in LMA was explained by light ($p < 0.001$, Appendix, Fig. 3).

Light environment had no effect on LMA at three narrow bands of height (Fig. 5A-C), but LMA significantly increased with height within three narrow bands of light environment (Fig. 5D-F). The variance inflation factor (VIF) between height and ln(light) was 1.9. Since this value is close to 1, we conclude that we do not have a serious problem of collinearity between height and ln(light) (Chatterjee and Price 1991) .

DISCUSSION

LMA pattern within the canopy is not the result of species replacement

We set out to determine what the primary driving forces were in the leaf mass per area of all functional groups in an old growth tropical rainforest. We randomly sampled the canopy in both horizontal and vertical dimensions; therefore, mean sample heights should indicate where the majority of leaves of each functional group were located in the canopy profile (Fig. 1). If species replacement were driving the pattern of increasing LMA within the canopy profile, we would expect to find species at the bottom of the profile to have lower LMA than species at the top of the profile. Palms (22% of total LAI, Clark et al. 2008) had the largest overall LMA, but were primarily located in the lower canopy (Fig. 1). If the life form spectrum was dictating vertical LMA patterns, we would also expect that lianas, located almost exclusively in the upper canopy, would have the highest LMA values. This was not the case. The change in life form does not correspond with the change in LMA within the canopy, indicating that the trend of increasing LMA within the canopy profile was not driven by a genotypic pattern of species replacement.

Height is the primary driver of the LMA gradient, but light also has some effect

LMA was much more strongly related to height than to light in this forest. In fact, the data show an incredible uniformity of pattern with height across all species sampled (Fig. 2C). Piece-wise regression results and plots of mean LMA vs. light suggest that light does play a role in controlling leaf morphology at 0-18 % of diffuse transmittance where the relationship between light and LMA is linear and less variable (Fig. 2B,D). Our results correspond with a recent study in tall sequoias, where LMA increased continuously with height, but did not respond to increasing light levels above about 20%

canopy openness (Ishii et al. 2008). Several additional studies have also suggested that the plastic response of foliar morphology to light levels may be constrained by water relations at the tops of very tall trees (Ishii et al. 2007, Meinzer et al. 2008, Ambrose et al. 2009). Chabot et al. (1979) hypothesized a plateau in LMA response when photon flux densities are saturating for photosynthesis, and Ellsworth and Reich (1992) found all or most of the photosynthetic acclimation to high light in sugar maple to occur at 15% of full sunlight.

Several recent studies have suggested that light may not be the primary driving force behind vertical gradients of LMA in forest canopies (Niinemets and Kull 1995, Niinemets 1997, Niinemets and Kull 1998, Rijkers et al. 2000, Marshall and Monserud 2003, Koch et al. 2004, Woodruff et al. 2004, England and Attiwill 2006, Ryan et al. 2006, Burgess and Dawson 2007, Ishii et al. 2007, Ishii et al. 2008, Meinzer et al. 2008). What mechanism could explain this phenomenon of a tight relationship between LMA and height for all species in a forest? Xylem water potential decreases by 0.01 MPa per meter of height, simply because of gravity (Scholander et al. 1965). Leaf turgor pressure has also been found to decrease with height in trees (Woodruff et al. 2004, Meinzer et al. 2008), likely as a response to the decrease in leaf water potential due to both gravity and hydraulic path length. Recent studies have found that leaves expand and develop primarily at night (Matsubara et al. 2006, Schurr et al. 2006), when water potential and turgor pressure are highest. Nighttime water potential and turgor pressure values are most likely to be linearly related to height because the effects of gravitational potential dominate at night (Scholander et al. 1965). Decreased turgor pressure will cause decreased cell expansion (Hsiao 1973), which could result in denser, smaller foliage and higher LMA with each meter of height increase. It is possible that osmotic and stomatal adjustment could also dynamically affect xylem and leaf water potential, but these forces are minimized at night when transpiration is low or absent. Thus, LMA may overall be responding more strongly to leaf water potential than to light environment, especially in the tops of tall trees.

In contrast to our results, some studies have reported linear relationships between LMA and light over a wide range of light conditions. It is possible that these studies did not show curved relationships because they did not have enough data points in the high light range (Ellsworth and Reich 1993, Niinemets and Tenhunen 1997), or because they were conducted on shorter, open-grown trees where the light vs. LMA relationship may not yet have reached an asymptote (Dejong and Doyle 1985, Sack et al. 2006). In fact, Niinemets et al. (1998) hypothesized that LMA in shade tolerant trees had a linear relationship with light while shade-intolerant trees showed a curved relationship with light because the plasticity of the shade intolerant species had not yet reached saturation levels.

Epiphytes show a different pattern

The height vs. LMA relationship was weaker for epiphytes than any other functional group (Table 1, Fig. 3E,O), and the "light only" model performed better than the "height only" model for epiphytes alone (Fig. 4). Epiphytic leaves usually develop in canopy soils with no hydraulic connectivity to the ground. Therefore, water would not need to move from the ground up to the leaves, and gravity would have no effect on differences in turgor pressure or xylem water potential. These factors would circumvent the link between height and LMA and explain the weak relationship between LMA and height for this functional group. Koch et al. (2004) observed a similar phenomenon in redwoods, where an epiphytic redwood seedling high in the canopy had much lower LMA than adjacent foliage of the parent tree.

Other possible mechanisms

LMA undoubtedly responds to a suite of environmental and genetic pressures (in addition to the effects of height), which are all together responsible for the morphology of each leaf. LMA could be responding to other environmental gradients which change within the canopy profile, such as humidity or temperature. These variables are not linear with height within the canopy, however, and are unlikely to be influencing LMA to have a linear response to height (temperature and relative humidity vs. height description based on towers project data, M. Ryan, unpublished). Carbon source vs. sink behavior could also affect foliar growth and morphological development in different parts of the canopy. For example, variation in leaf morphology could be an indirect effect of light environment if a leaf were in a low light environment (sink) but surrounded by leaves in higher light environment (sources), or vice versa, but this is unlikely to result in a linear pattern with height. Niinemets found that solutes increased in higher leaves, and concluded that this may be in part responsible for greater LMA in needles higher in the canopy (Niinemets 1997). Very little is known about these secondary environmental responses in LMA.

Our data showed that LMA was related to sample height, which is related to but not the same as total plant height. The proportion of juveniles likely decreases with height, and in general, juveniles (seedlings in particular) can have lower LMA than adults. LMA could also change ontogenetically with total plant size independent of light or leaf water potential. Differences in LMA with total tree height have been found in tropical and conifer forests (Niinemets and Kull 1995, Rijkers et al. 2000, Kenzo et al. 2006), though it is difficult to determine if these patterns are the result of gravity or developmental constraints on plasticity, which is much less understood.

Implications for physiological function

Within forest canopies, LMA is predictive of gas exchange rates and foliar nutrients per unit leaf area because of the strong correlation of LMA with height, and the influence of LMA on rates per unit area (Ellsworth and Reich 1993, Mitchell et al. 1999, Meir et al. 2001, Cavaleri et al. 2008). The remarkable LMA-height relationship has the potential to greatly improve and simplify canopy process models. Height is much easier to measure than light, and it may be possible to solely use height to model the foliar physiological parameters that correlate with LMA within canopy profiles, such as photosynthetic capacity (Ellsworth and Reich 1993), foliar nitrogen (Ellsworth and Reich 1993, Mitchell et al. 1999, Meir et al. 2001, Cavaleri et al. 2008), foliar phosphorous (Meir et al. 2001, Cavaleri et al. 2008), and dark respiration (Mitchell et al. 1999, Meir et al. 2001, Cavaleri et al. 2008). Light detection and ranging (LIDAR) technology can directly measure canopy height profiles remotely (Lefsky et al. 2002), potentially simplifying the remote sensing of canopy physiology.

CONCLUSION

In this study, we measured light environment, height, and LMA of all plant functional groups (200+ species) found along 45 vertical canopy transects across the landscape of an old-growth tropical rain forest in Costa Rica. We concluded that the vertical pattern of LMA was not the result of species replacement. While light did affect LMA, especially in the light-limited understory below 18 m and 22 % diffuse transmittance, LMA was better related to height throughout the entire canopy profile. Our results support the hypothesis that the universal LMA gradient within forest stands is likely driven by a linear decrease in turgor pressure with height, caused by a linear decrease in xylem water potential with gravity. LMA is easily measurable and remarkably predictive of foliar physiological function, within and across species.

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LITERATURE CITED

Ambrose, A. R., S. C. Sillett, and T. E. Dawson. 2009. Effects of tree height on branch hydraulics, leaf structure and gas exchange in California redwoods. Plant Cell and Environment 32:743-757.

Bond, B. J., B. T. Farnsworth, R. A. Coulombe, and W. E. Winner. 1999. Foliage physiology and biochemistry in response to light gradients in conifers with varying shade tolerance. Oecologia 120:183-192.

Burgess, S. S. O., and T. E. Dawson. 2007. Predicting the limits to tree height using statistical regressions of leaf traits. New Phytologist 174:626-636.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, NY, USA.

Cavaleri, M. A., S. F. Oberbauer, and M. G. Ryan. 2008. Foliar and ecosystem respiration in an old-growth tropical rain forest. Plant, Cell and Environment 31:473–483.

Chabot, B. F., T. W. Jurik, and J. F. Chabot. 1979. Influence of instantaneous and integrated light-flux density on leaf anatomy and photosynthesis. American Journal of Botany 66:940-945.

Chatterjee, S., and B. Price. 1991. Regression Diagnostics. John Wiley, New York.

Clark, D. B., P. C. Olivas, S. F. Oberbauer, D. A. Clark, and M. G. Ryan. 2008. First direct landscape-scale measurement of tropical rain forest Leaf Area Index, a key driver of global primary productivity Ecology Letters 11:163-172.

Clark, M. L., D. B. Clark, and D. A. Roberts. 2004. Small-footprint lidar estimation of sub-canopy elevation and tree height in a tropical rain forest landscape. Remote Sensing of Environment 91:68-89.

Dejong, T. M., and J. F. Doyle. 1985. Seasonal relationships between leaf nitrogen content (photosynthetic capacity) and leaf canopy light exposure in peach (*Prunus persica*). Plant Cell and Environment 8:701-706.

Ellsworth, D. S., and P. B. Reich. 1992. Leaf mass per area, nitrogen-content and photosynthetic carbon gain in *Acer saccharum* seedlings in contrasting forest light environments. Functional Ecology 6:423-435.

Ellsworth, D. S., and P. B. Reich. 1993. Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. Oecologia 96:169-178.

England, J. R., and P. M. Attiwill. 2006. Changes in leaf morphology and anatomy with tree age and height in the broadleaved evergreen species, Eucalyptus regnans F. Muell. Trees-Structure and Function 20:79-90.

Gendron, F., C. Messier, and P. G. Comeau. 1998. Comparison of various methods for estimating the mean growing season percent photosynthetic photon flux density in forests. Agricultural and Forest Meteorology 92:55-70.

Hanson, H. C. 1917. Leaf structure as related to environment. American Journal of Botany 4:533-560.

Hartshorn, G. S. 1983. Plants. Pages 118-157 *in* D. H. Janzen, editor. Costa Rican Natural History. University of Chicago Press, Chicago.

Hikosaka, K., I. Terashima, and S. Katoh. 1994. Effects of leaf age, nitrogen nutrition and photon flux-density on the distribution of nitrogen among leaves of a vine grown horizontally to avoid mutual shading of leaves. Oecologia 97:451-457.

Hollinger, D. Y. 1989. Canopy organization and foliage photosynthetic capacity in a broad-leaved evergreen montane forest. Functional Ecology 3:53-62.

Hsiao, T. C. 1973. Plant responses to water stress. Annual Review of Plant Physiology and Plant Molecular Biology 24:519-570.

Hutchison, B. A., D. R. Matt, R. T. McMillen, L. J. Gross, S. J. Tajchman, and J. M. Norman. 1986. The architecture of a deciduous forest canopy in eastern Tennessee, USA. Journal of Ecology 74:635-646.

Ishii, H., S. Kitaoka, T. Fujisaki, Y. Maruyama, and T. Koike. 2007. Plasticity of shoot and needle morphology and photosynthesis of two Picea species with different site preferences in northern Japan. Tree Physiology 27:1595-1605.

Ishii, H. T., G. M. Jennings, S. C. Sillett, and G. W. Koch. 2008. Hydrostatic constraints on morphological exploitation of light in tall Sequoia sempervirens trees. Oecologia 156:751-763.

Jackson, L. W. R. 1967. Effect of shade on leaf structure of deciduous tree species. Ecology 48:498-499.

Kenzo, T., T. Ichie, Y. Watanabe, R. Yoneda, I. Ninomiya, and T. Koike. 2006. Changes in photosynthesis and leaf characteristics with tree height in five dipterocarp species in a tropical rain forest. Tree Physiology 26:865-873.

Koch, G. W., S. C. Sillett, G. M. Jennings, and S. D. Davis. 2004. The limits to tree height. Nature 428:851-854.

Lefsky, M. A., W. B. Cohen, G. G. Parker, and D. J. Harding. 2002. Lidar remote sensing for ecosystem studies. BioScience 52:19-30.

Lieberman, D., M. Lieberman, R. Peralta, and G. S. Hartshorn. 1996. Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. Journal of Ecology 84:137-152.

Marshall, J. D., and R. A. Monserud. 2003. Foliage height influences specific leaf area of three conifer species. Canadian Journal of Forest Research 33:164-170.

Matsubara, S., V. Hurry, N. Druart, C. Benedict, I. Janzik, A. Chavarria-Krauser, A. Walter, and U. Schurr. 2006. Nocturnal changes in leaf growth of *Populus deltoides* are controlled by cytoplasmic growth. Planta 223:1315-1328.

McDade, L., K. Bawa, G. Hartshorn, and H. Hespenheide. 1994. La Selva: the ecology and natural history of a neotropical rainforest. Chicago Press, Chicago.

Meinzer, F. C., B. J. Bond, and J. A. Karanian. 2008. Biophysical constraints on leaf expansion in a tall conifer. Tree Physiology 28:197-206.

Meir, P., J. Grace, and A. C. Miranda. 2001. Leaf respiration in two tropical rainforests: constraints on physiology by phosphorus, nitrogen and temperature. Functional Ecology 15:378-387.

Mitchell, K. A., P. V. Bolstad, and J. M. Vose. 1999. Interspecific and environmentally induced variation in foliar dark respiration among eighteen southeastern deciduous tree species. Tree Physiology 19:861-870.

Niinemets, U. 1997. Distribution patterns of foliar carbon and nitrogen as affected by tree dimensions and relative light conditions in the canopy of *Picea abies*. Trees 11:144-154.

Niinemets, U., and O. Kull. 1995. Effects of light availability and tree size on the architecture of assimilative surface in the canopy of *Picea abies* - variation in shoot structure. Tree Physiology 15:791-798.

Niinemets, U., and O. Kull. 1998. Stoichiometry of foliar carbon constituents varies along light gradients in temperate woody canopies: implications for foliage morphological plasticity. Tree Physiology 18:467-479.

Niinemets, U., and J. D. Tenhunen. 1997. A model separating leaf structural and physiological effects on carbon gain along light gradients for the shade-tolerant species *Acer saccharum*. Plant Cell and Environment 20:845-866.

Nobel, P. S. 1977. Internal leaf area and cellular CO_2 resistance - photosynthetic implications of variations with growth-conditions and plant species. Physiologia Plantarum 40:137-144.

Oberbauer, S. F., and B. R. Strain. 1986. Effects of canopy position and irradiance on the leaf physiology and morphology of *Pentaclethra macroloba* (Mimosaceae). American Journal of Botany 73:409-416.

Oquist, G., L. Brunes, and J. E. Hallgren. 1982. Photosynthetic efficiency of *Betula pendula* acclimated to different quantum flux densities. Plant Cell and Environment 5:9-15.

Reich, P. B., C. Uhl, M. B. Walters, and D. S. Ellsworth. 1991. Leaf life-span as a determinant of leaf structure and function among 23 Amazonian tree species. Oecologia 86:16-24.

Rijkers, T., T. L. Pons, and F. Bongers. 2000. The effect of tree height and light availability on photosynthetic leaf traits of four neotropical species differing in shade tolerance. Functional Ecology 14:77–86.

Ryan, M. G., N. Phillips, and B. J. Bond. 2006. The hydraulic limitation hypothesis revisited. Plant Cell and Environment:367-381.

Sack, L., P. J. Melcher, W. H. Liu, E. Middleton, and T. Pardee. 2006. How strong is intracanopy leaf plasticity in temperate deciduous trees? American Journal of Botany 93:829-839.

Scholander, P. F., H. T. Hammel, E. D. Bradstreet, and E. A. Hemmingsen. 1965. Sap pressure in vascular plants - negative hydrostatic pressure can be measured in plants. Science 148:339-346.

Schurr, U., A. Walter, and U. Rascher. 2006. Functional dynamics of plant growth and photosynthesis - from steady-state to dynamics - from homogeneity to heterogeneity. Plant Cell and Environment 29:340-352.

Smith, W. K., and P. S. Nobel. 1978. Influence of irradiation, soil-water potential, and leaf temperature on leaf morphology of a desert broadleaf, *Encelia farinosa gray* (Compositae). American Journal of Botany 65:429-432.

Woodruff, D. R., B. J. Bond, and F. C. Meinzer. 2004. Does turgor limit growth in tall trees? Plant Cell and Environment 27:229-236.

TABLES

Table 1. For each plant functional group and all groups pooled together, regression coefficients, R^2 values, and Akaike's Information Criterion (AIC, lower is better) are displayed for the log-linear regressions between LMA and light, the linear regressions between LMA and height, and the multiple regressions including both terms (the interaction term was not significant in any case and subsequently dropped). Partial R^2 values represent the differences in R^2 between the full model and each single-parameter model.

		Light only LMA = $\beta_0 + \beta_1$ ln(light)				Height only LMA = $\beta_0 + \beta_1$ height				Height and Light LMA = $\beta_0 + \beta_1$ ln(light) + β_2 height					Partial R^2 for adding ln(light)	Partial R^2 for adding height
Functional Group	n	β_0	β_1	R^2	AIC	β_0	β_1	R^2	AIC	β_0	β_1	β_2	R^2	AIC		
Trees	542	58**	14**	0.26	3854	44**	2.8**	0.44	3706	43**	2.6*	2.5**	0.44	3703	0.01	0.18
Lianas	164	61**	10**	0.22	1105	41**	2.5**	0.52	1027	40**	N.S.	2.4**	0.52	1028	<0.01	0.30
Palms	197	78**	14**	0.26	1364	68**	3.4**	0.40	1324	66**	5.8**	2.7**	0.42	1317	0.03	0.16
Herbaceous groups	157	49**	6.6**	0.07	1061	44**	2.0**	0.27	1023	47**	-5.2*	2.6**	0.29	1020	0.02	0.22
Epiphytes	202	53**	17**	0.10	3872	60**	2.1**	0.10	3895	52**	N.S.	N.S.	0.11	3853	0.01	0.01
All groups	1262	61**	12**	0.16	9343	53**	2.4**	0.27	9173	52**	2.4*	2.1**	0.27	9170	<0.01	0.11

** p-value < 0.01;
* p-value < 0.05;
N.S. p-value > 0.05

FIGURE LEGENDS

Figure 1. Mean sample height at which each functional group was randomly sampled (plot A), and mean LMA of each functional group (plot B). Error bars indicate standard error of the mean.

Figure 2. LMA vs. sample height (plot A), and LMA vs. light environment (plot B) for all functional groups pooled together; and mean LMA values aggregated into bins of height class (plot C), and bins of light class (plot D). Error bars represent standard errors in the X and Y direction of between 37 (greater height) and 314 individuals (lower height) per height class, and between 11 (mid light) and 547 individuals (lower light) per light class. Error bars in the X direction are obscured by the symbols. Plot D shows two model fits to the mean data, a logarithmic model (solid line) and a linear piecewise regression (dotted line). $P<0.0001$ for all.

Figure 3. For each individual functional group, mean LMA values were aggregated into bins of height class (plots A-E), and bins of light class (plots K-O); and all data points were plotted for LMA vs. sample height (plots F-J), and LMA vs. light (plots P-T). LMA increased linearly with height for all functional groups (plots F-J), and the non-linear relationship between LMA and light was described by a logarithmic regression for each functional group (plots P-T). See Table 1 for regression equation coefficients, for all models: p-values <0.001. Error bars in mean LMA plots (A-E and K-O) represent standard errors in the X and Y direction, although many of the error bars are obscured by the symbols.

Figure 4. For all functional groups pooled, LMA was plotted against ln light for three narrow bands of height (plots A-C), and against height for three narrow bands of

light (plots D-F). Figures show no change in LMA with light at three height levels, but significant increase in LMA with height at three light levels.

Figure 5. Standardized Akaike's Information Criterion (Model AIC – $\mathrm{AIC}_{\mathrm{min}}$) for each of three competing linear models predicting LMA for the following functional groups: trees, lianas, palms, herbaceous groups, and epiphytes. For each group, AIC-$\mathrm{AIC}_{\mathrm{min}}$ is zero for the best fit model. The three models were: LMA = $\beta_0 + \beta_1$ ln(light); LMA = $\beta_0 + \beta_1$ height; and LMA = $\beta_0 + \beta_1$ height $+ \beta_2$ ln(light). For all groups except epiphytes, once height is included in the model, ln(light) does not greatly improve the model fit. The model with ln(light) only is the worst fit for all groups except epiphytes

FIGURES

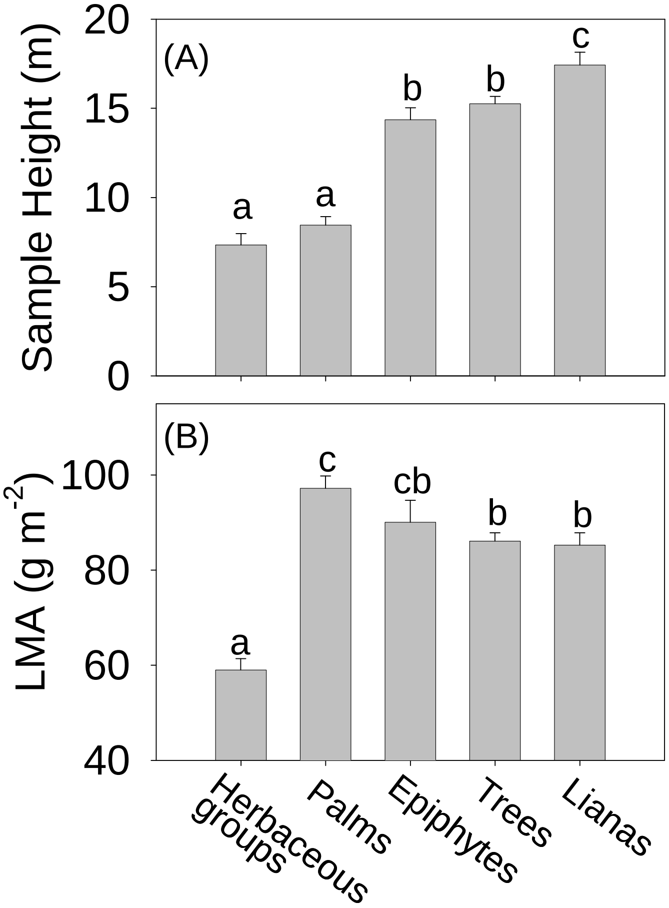

Fig. 1

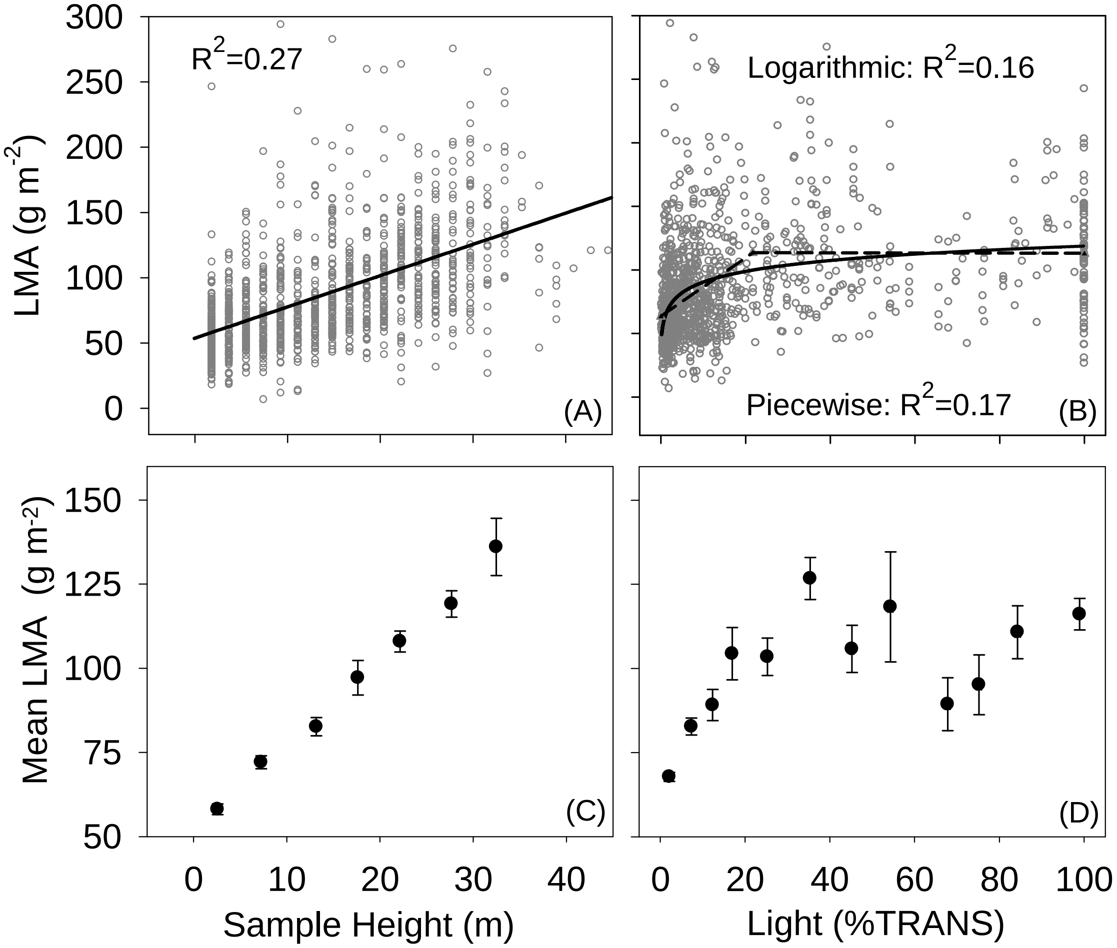
R^2=0.27
Logarithmic: R^2=0.16
Piecewise: R^2=0.17
LMA (g m^{-2})
300
250
200
150
100
50
0
(A)
(B)
Mean LMA (g m-2)
150
125
100
75
50
(C)
(D)
0
10
20
30
40
Sample Height (m)
0
20
40
60
80
100
Light (%TRANS)

Fig. 2

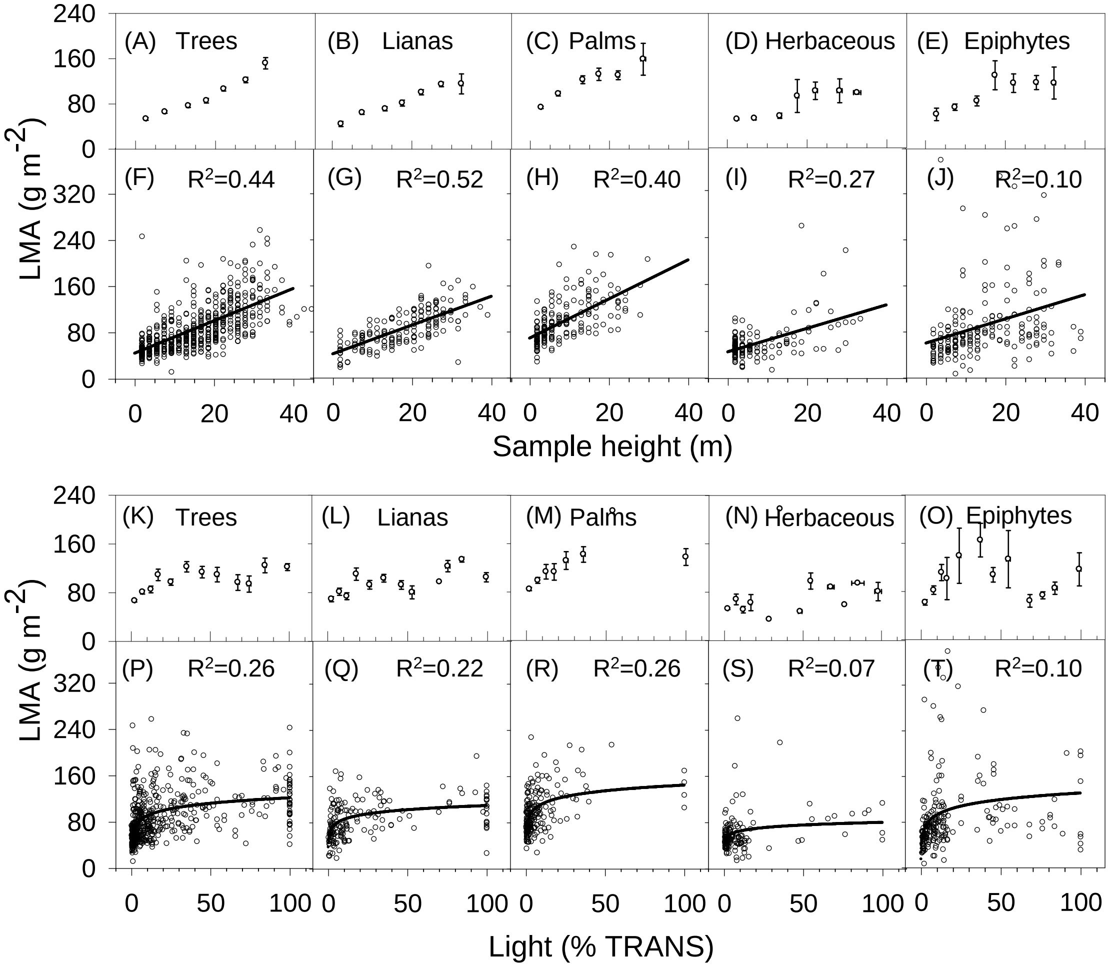
(A) Trees
(B) Lianas
(C) Palms
(D) Herbaceous
(E) Epiphytes
(F) R²=0.44
(G) R²=0.52
(H) R²=0.40
(I) R²=0.27
(J) R²=0.10
LMA (g m-2)
0
80
160
240
320
0
20
40
Sample height (m)
(K) Trees
(L) Lianas
(M) Palms
(N) Herbaceous
(O) Epiphytes
(P) R²=0.26
(Q) R²=0.22
(R) R²=0.26
(S) R²=0.07
(T) R²=0.10
0
50
100
Light (% TRANS)

Fig. 3

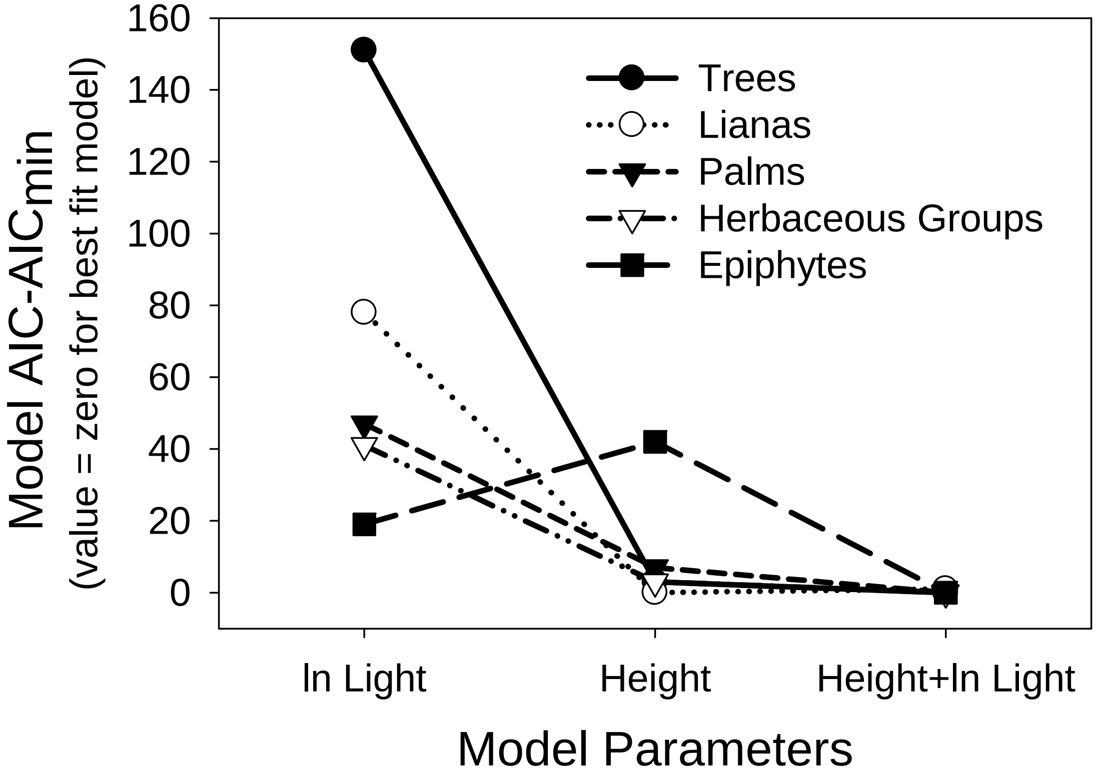
160
140
120
100
80
60
40
20
0
Model AIC-AIC$_{min}$
(value = zero for best fit model)
Trees
Lianas
Palms
Herbaceous Groups
Epiphytes
ln Light
Height
Height+ln Light
Model Parameters

Fig. 4

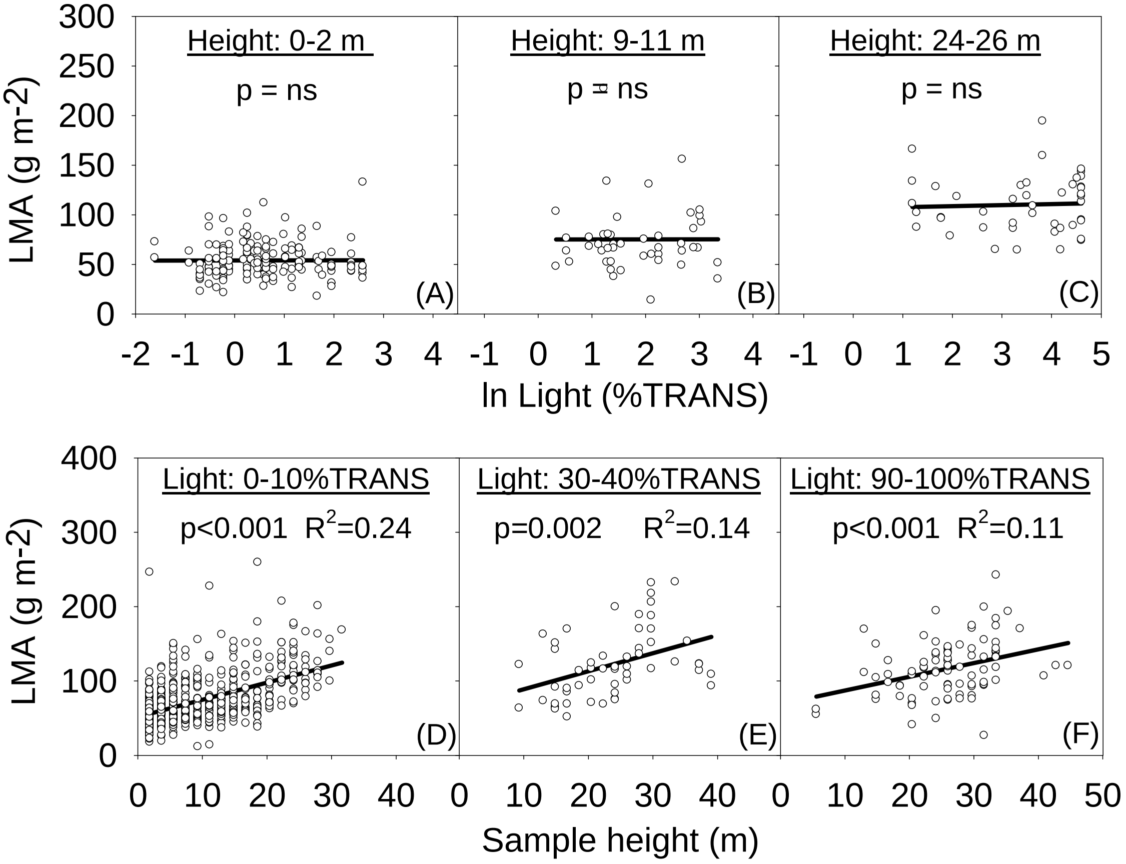
Height: 0-2 m
p = ns
Height: 9-11 m
p = ns
Height: 24-26 m
p = ns
(A)
(B)
(C)
LMA (g m-2)
300
250
200
150
100
50
0
-2 -1 0 1 2 3 4 -1 0 1 2 3 4 -1 0 1 2 3 4 5
ln Light (%TRANS)
Light: 0-10%TRANS
p<0.001 R2=0.24
Light: 30-40%TRANS
p=0.002 R2=0.14
Light: 90-100%TRANS
p<0.001 R2=0.11
(D)
(E)
(F)
LMA (g m-2)
400
300
200
100
0
0 10 20 30 40 0 10 20 30 40 0 10 20 30 40 50
Sample height (m)

Fig. 5